

TIME-DEPENDENT CHANGES IN CONDITIONED SUPPRESSION

R. C. HOWARD¹ AND MARK RILLING

MICHIGAN STATE UNIVERSITY

Time-dependent changes in a response following aversive conditioning were investigated using a conditioned suppression procedure in a within-subjects design. Four groups of pigeons received Pavlovian conditioning "off the baseline", immediately followed by an operant task. During the Pavlovian phase, two groups received a forward pairing of a tone with shock, one group received a backward pairing, and one group received a truly random pairing. One of the forward pairing groups also received a delay between the Pavlovian and operant phases. For all groups, key pecking was reinforced on a variable-interval schedule during the operant phase. Testing sessions were identical to training sessions, except that the tone used during Pavlovian conditioning was presented either 0, 15, 30, 45, or 60 minutes after the operant phase began. Testing sessions in which the Pavlovian phase was omitted were also included. The results showed suppression to change as a function of the retention interval, with maximum suppression occurring at intermediate intervals. This U-shaped function was obtained for 11 of the 12 pigeons in the forward-pairing groups and for three of the five in the truly random group. Pigeons in the background pairing group did not show changes in suppression as a function of the retention interval.

Key words: Kamin effect, conditioned suppression, Pavlovian conditioning, operant conditioning, within-subjects design, pigeons

In most studies of learning, retention is a monotonically declining function of the amount of time since original learning. An exception to this rule is the U-shaped function, known as the Kamin effect, obtained following aversive conditioning with infra-human organisms. Kamin (1957) incompletely trained rats to avoid shock in a shuttle-box apparatus using a tone as the conditional stimulus (CS). Following this training, the subjects were divided into groups. One was immediately given additional training on the shuttlebox task and the other groups received delays between initial and subsequent conditioning that ranged from 30 min to 17 days. The mean number of avoidance responses during retraining was used as the measure of performance. The results showed a decline in successful avoidance responses up to a 1-hr delay

period. Groups with delay intervals longer than 1 hr showed progressively higher successful avoidance responses. For a 24-hr delay group, the number of avoidance responses did not differ significantly from the group retrained immediately. When performance was plotted as a function of the delay interval, a U-shaped function was obtained, with the greatest deficit in performance occurring at the 1-hr delay interval.

The Kamin effect is always measured as a change in performance obtained after various retention intervals following the occurrence of aversive conditioning (Anisman, 1975; Brush, 1971; Klein and Spear, 1970). The function reflects changes in the ability of an organism to learn or perform an avoidance response. It is reasonable to assume, however, that if an organism's response to a CS used in Pavlovian aversive conditioning was measured over time, a U-shaped function would also be obtained.

To determine if time-dependent changes in an organism's reaction to a CS occurs, it is necessary to use a procedure that does not require a specific avoidance response. Conditioned suppression, a decrease in the rate of an operant response during the presentation of an aversive CS, fulfills this requirement. Hunt

¹This research is based on a dissertation submitted by the first author to Michigan State University in partial fulfillment of the MA degree. The first author would like to thank Daniel F. Tortora and M. Ray Denny for their substantial contributions on the unpublished research referred to in the introduction. Reprints may be obtained from R. C. Howard, Department of Psychology, Olds Hall, Michigan State University, East Lansing, Michigan 48823.

and Brady (1951) developed a variation of the conditioned suppression procedure, known as "off-the-baseline" conditioned suppression, in which aversive Pavlovian conditioning occurs before testing the CS on an operant baseline. This method permits the manipulation of the retention interval between classical conditioning and testing of the CS on an operant baseline.

An "off-the-baseline" procedure has been used by McMichael (1966) and Tarpy (1966) to measure time-dependent changes in the level of conditioned suppression. In both experiments, rats received avoidance training in a shuttle-box, followed after various retention intervals by testing in an operant chamber. Testing consisted of the presentation of the tone used in avoidance training while lever pressing was reinforced with food. Their results showed a monotonic increase in conditioned suppression as a function of the retention interval. The failure of these studies to obtain a U-shaped function led Brush (1971) to conclude tentatively that a U-shaped function is not obtained when a conditioned suppression procedure is employed.

In an unpublished study from this lab, rats received suppression tests on an appetitive baseline at various intervals following shuttle-box training. The primary difference between this study and the McMichael (1966) and Tarpy (1966) studies involved the procedure used during the retention interval. In both previous studies, the rat spent the retention interval in a holding cage, the end of the retention interval occurring with placement of the rat in the operant chamber. In the pilot study, the rat was placed, at the end of shuttle-box training, into the operant chamber and was free to bar press for food. At the end of the retention interval, a single suppression test was conducted. Using this procedure, a U-shaped function was obtained with maximum suppression occurring at intermediate retention intervals. This increase in suppression is opposite to the decrease in performance at intermediate retention intervals obtained in Kamin's study (Kamin, 1957).

The purpose of the present study was to determine for pigeons the function relating conditioned suppression to retention interval. The CS was established through Pavlovian conditioning to prevent any problems resulting from the acquisition of an avoidance re-

sponse during the training phase. To avoid any problems resulting from conducting training in a chamber different from the one used in testing, pigeons received both training and testing in the same chamber. Most subjects worked on an operant task for food reinforcement during the retention interval. Pigeons were selected as the experimental organisms because of the paucity of data on the "Kamin effect" with this species.

In contrast with most previous studies on the "Kamin effect", the present study used a within-subjects design to permit an evaluation of time-dependent changes in conditioned suppression for individual pigeons. Klein and Spear (1973) also used a within-subjects design to investigate the "Kamin effect", but reported only group averages.

The present design consisted of an experimental group and three control groups. The experimental group received a tone followed immediately by shock during Pavlovian conditioning. To ensure that subsequent suppression of operant responding during the tone was the result of the pairing of the tone with shock, control groups were necessary. The traditional control group in Pavlovian conditioning has been a backward pairing of the CS with the US. However, Rescorla (1969) argued that a CS that follows a US may become inhibitory because it predicts the absence of the US for a period of time. He suggested a truly random correlation of the CS with the US as the appropriate control condition. In a truly random control procedure, the probability of the US in the presence of the CS is equal to the probability of the US in the absence of the CS. Although Rescorla predicted that conditioning to the CS would not occur using such a truly random procedure, Benedict and Ayres (1972), Kremer and Kamin (1971), and Quinsey (1971) demonstrated conditioning following truly random CS-US pairings. Rescorla (1972) later predicted that excitatory conditioning could occur using the truly random procedure, but that with extended training, conditioning would dissipate. Given this lack of consensus about the appropriate control group, both the traditional backward pairing control group and the truly random control group were used in the present study. The appropriate control group should fail to demonstrate time-dependent changes in conditioned suppression, thereby producing a flat function.

A third control group received forward pairings of tone with shock during the Pavlovian phase identical to the experimental group. In this group, however, the appetitive baseline was not available until just before the end of the retention interval. The appetitive baseline, for this group, did not begin until 4 min before presentation of the tone for testing. The purpose of this group was to assess the notion, mentioned above, that the conditions during the retention interval accounted for the difference between our pilot study and those of McMichael (1966) and Tarpy (1966). If the availability of the operant task was critical for the appearance of time-dependent changes in conditional suppression, then the control group should not show U-shaped functions.

METHOD

Subjects

Twenty-four White Carneaux pigeons were maintained at 80% of their free-feeding weights. The pigeons were housed in individual cages and had free access to grit and water. The colony in which the pigeons were housed was continually illuminated by standard fluorescent ceiling lights. Each pigeon was implanted with stainless-steel electrodes through each side of the pubic arch. These electrodes were connected to a phono plug on a leather harness worn by the pigeon (Azrin, 1969).

Apparatus

Two standard, three-key, Lehigh Valley Electronics experimental chambers were used. The center key of each chamber was illuminated with a black vertical line on a white background or a green stimulus. The stimuli were projected onto the key using an Industrial Electronics Engineers inline projector (Model #10-0W78-1820-L). A houselight, consisting of a GE #1820 lamp, remained on during the sessions. A GE #1820 lamp illuminated the food hopper during reinforcement. The onset of reinforcement was controlled by a Lehigh Valley Electronics Photosensor (Model #221-10). A speaker, mounted on the front panel of the operant chamber was used to present the auditory stimulus. A B&K sound-pressure meter was used to set the auditory stimulus at 65 dB re 20μ N/m² above the ambient noise level. The chamber was modified for shock delivery

as described by Klein and Rilling (1974). A high internal resistance ac milliamper power supply, insensitive to external resistance changes up to 5000 ohms, was used as the shock source. A fan, providing masking noise and ventilation, remained on during the sessions. The chambers were maintained in separate rooms separated by a central room in which scheduling and recording equipment was maintained.

Procedure

Pretraining. The pigeons were initially magazine trained and autoshaped to peck the center key. An autoshaping trial consisted of the illumination of the key with the green stimulus for 8 sec, followed by access to a grain-filled hopper for 3.5 sec. The intertrial interval between autoshaping trials was varied, with a mean of 2 min. Each session of autoshaping was 60 min in duration and was terminated when a pigeon emitted 100 or more responses to the green stimulus during a session for two consecutive sessions.

After autoshaping, the pigeons received one 60-min session on a variable-interval (VI) 30-sec schedule followed by two 60-min sessions on VI 60-sec. Next, the pigeon received two, 60-min sessions on a VI 60-sec schedule of reinforcement during which a 1000-Hz tone, 2 min in duration, was presented on a variable intertrial interval schedule with an average duration of 2 min. During all sessions in which a pigeon pecked for reinforcement, the key was illuminated with the green stimulus.

Training. Following pretraining, the pigeons were divided into four groups: (a) a forward pairing group, (b) a forward pairing with operant delay group, (c) a backward pairing group, and (d) a truly random group. Each group contained six pigeons.

A training session consisted of two phases, a Pavlovian conditioning phase and an operant conditioning phase. In the Pavlovian phase, the pigeons received presentations of a 1000-Hz tone and a 2-mA shock. In the operant phase, the pecking response was reinforced on a VI 60-sec schedule. Grain was never available during the Pavlovian phase and shocks never occurred during the operant phase.

The onset of the Pavlovian phase was signalled by the illumination of the houselight. The duration of the 1000-Hz tone was 2 min and the duration of the 2-mA shock was 1.5

sec. For the forward pairing group and the forward pairing with operant delay group, presentation of the tone was immediately followed by shock. The intertrial interval (ITI) was varied following a VI 2-min schedule. For the backward pairing group, a trial consisted of the presentation of shock followed, after a 10-sec delay, by the tone. The tone was followed by a 30-sec safe period before the next ITI began. The length of the ITI varied following a VI 2-min schedule. For the truly random group, tone and shock presentations were arranged on independent VI 2-min schedules. For all groups, the Pavlovian phase ended when the pigeon had received 15 presentations of tone and 15 presentations of shock.

At the end of the Pavlovian phase, the center key was illuminated with the green stimulus for all groups, except the forward pairing with operant delay group. During the operant phase, responding was reinforced on a VI 60-sec schedule. No tones or shocks occurred during this phase before testing. For the forward pairing with operant delay group, a delay between the Pavlovian and operant phases was imposed, indicated by the illumination of the center key with a vertical line stimulus. The delay period was either 0, 15, 30, 45, or 60 min in duration. The delay intervals were randomized across sessions, with each subject receiving two sessions at each delay interval; during the delay period, no shocks or tones were presented, nor was reinforcement for responding available. At the end of the delay interval, the key was illuminated with the green stimulus and responding was reinforced on the VI 60-sec schedule.

For all groups, the operant phase was 60 min. Each session consisted of a Pavlovian phase followed by an operant phase. There were 10 training sessions.

Testing. Testing sessions were identical to training sessions, with one exception. During the operant phase, the tone without shock was presented for 2 min either 4, 15, 30, 45, or 60 min from the beginning of the phase. The Pavlovian phase preceded the operant phase as in training. The tone was presented only once per session for testing during the operant phase. The schedule of reinforcement remained in effect during presentation of the tone. At least 24 hr intervened between testing sessions. For the forward pairing with operant delay group, the delay period was terminated

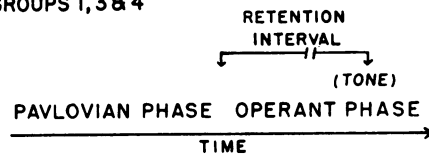
and the green stimulus illuminated, indicating availability of reinforcement for key pecking, 4 min before the scheduled tone presentation. The VI 60-sec schedule of reinforcement was made available 4 min before tone presentation to allow a period of warmup on the operant schedule before testing. For all groups, the retention interval was measured from the end of the Pavlovian phase to the tone presentation in testing. Therefore, the forward pairing with operant delay group did not receive a delay period for the 4-min testing interval. Figure 1 depicts the procedure used for all groups.

All groups also received test sessions in which the Pavlovian phase was omitted. These sessions were always 24 hr after a normal testing session. During these sessions, the tone was presented at one of the testing intervals and all testing intervals were sampled across pigeons.

The order of testing was randomized within and between pigeons, with all testing intervals sampled across pigeons per day. The randomized schedule of testing was replicated four times, giving each pigeon four tests at each interval. Each pigeon received a total of 24 testing sessions. Suppression ratios were calculated using Kamin's (1961) formula. The formula is:

$$\frac{T}{\text{pre } T + T} \quad (1),$$

GROUPS 1, 3 & 4



GROUP 2

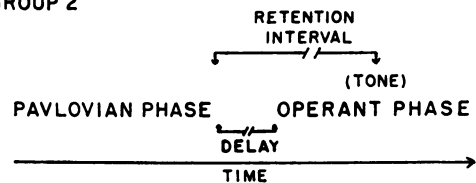


Fig. 1. A schematic of the procedure used during testing. The retention interval for all groups was varied between 4 min and 60 min. The delay interval for Group 2 was varied between 0 min and 56 min. (Group 1: forward pairing; Group 2: forward pairing with operant delay; Group 3: backward pairing; Group 4: truly random.)

where T is the number of responses emitted during the tone presentation and pre T is the number of responses emitted in the 2-min period preceding the tone presentation.

RESULTS

The results for the forward pairing group are shown in Figure 2. U-shaped functions, indicating an average maximum suppression at intermediate intervals, were obtained for five of the six pigeons in this group. The suppression ratio presented represents an average suppression ratio derived from ratios taken for each replication. The point of maximum suppression varied for individual pigeons, with the maximum for P4 and P6 occurring at 15 min, for P2 and P3 at 30 min, and for P1 at 45 min. For P5, the average suppression ratio did not result in a U-shaped function. The 1440-min interval on the graph represents the average suppression obtained during the sessions in which the Pavlovian phase was omitted. Although this testing interval is not equivalent to the other testing intervals, because pigeons did not receive Pavlovian conditioning before testing, it is included in the figures for convenience. Figure 3 shows the individual gradients obtained for each replication. It is interesting to note that P5 produced inverted U-shaped functions for replications one and two, which then inverted to the typical U-shaped function for replications three and four.

The results for the forward pairing with operant delay group are shown in Figure 4. U-shaped functions were obtained for each of the six pigeons, with maximum suppression occurring for P8 and P9 at 15 min, for P10 and P12 at 30 min, and for P7 and P11 at 45 min.

A two-factor, mixed design, analysis of variance was performed on the data from the two forward pairing groups. The test was conducted to determine if the level of suppression varied significantly as a function of the retention interval. The results showed a significant effect of the retention interval on the level of suppression ($F_{5,50} = 2.81$, $p < 0.025$). The two groups were also found to differ significantly in the total amount of suppression over all testing intervals ($F_{1,10} = 23.8$, $p < 0.001$). A comparison of the two groups showed suppression levels in the forward pairing group to be significantly higher than suppression levels in

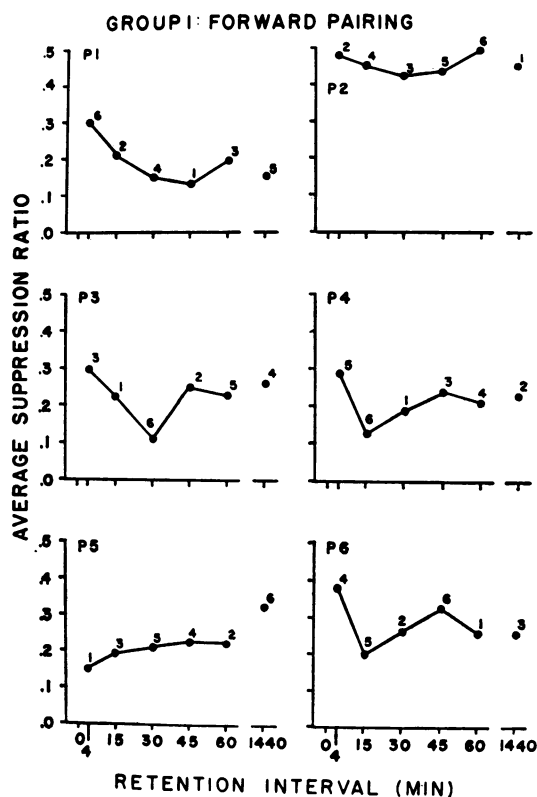


Fig. 2. The level of response suppression as a function of the testing interval for individual pigeons in the forward pairing group. Each point represents the average suppression ratio for the four tests. The order of testing for each pigeon is represented by the numbers above the data points.

the forward pairing with operant delay group (see Figures 2 and 4). The analysis of variance showed no significant interaction between the group tested and time-dependent changes in suppression ($F_{5,50} = 0.55$, $p > 0.10$).

A trend analysis was performed on the data to determine what type of function best fit the changes obtained in suppression as a function of the retention interval. The results showed that a quadratic, U-shaped function provided the best fit ($F_{1,50} = 6.35$, $p < 0.025$).

Table 1 shows the average response rates during the pretone period and during the tone for all groups. The table was derived from averaging within and across pigeons and suppression ratios cannot be obtained from the data. A two-factor, mixed design, analysis of variance was performed on the response rates during the pretone period for the two forward pairing groups. The test was performed to determine if any systematic changes in response

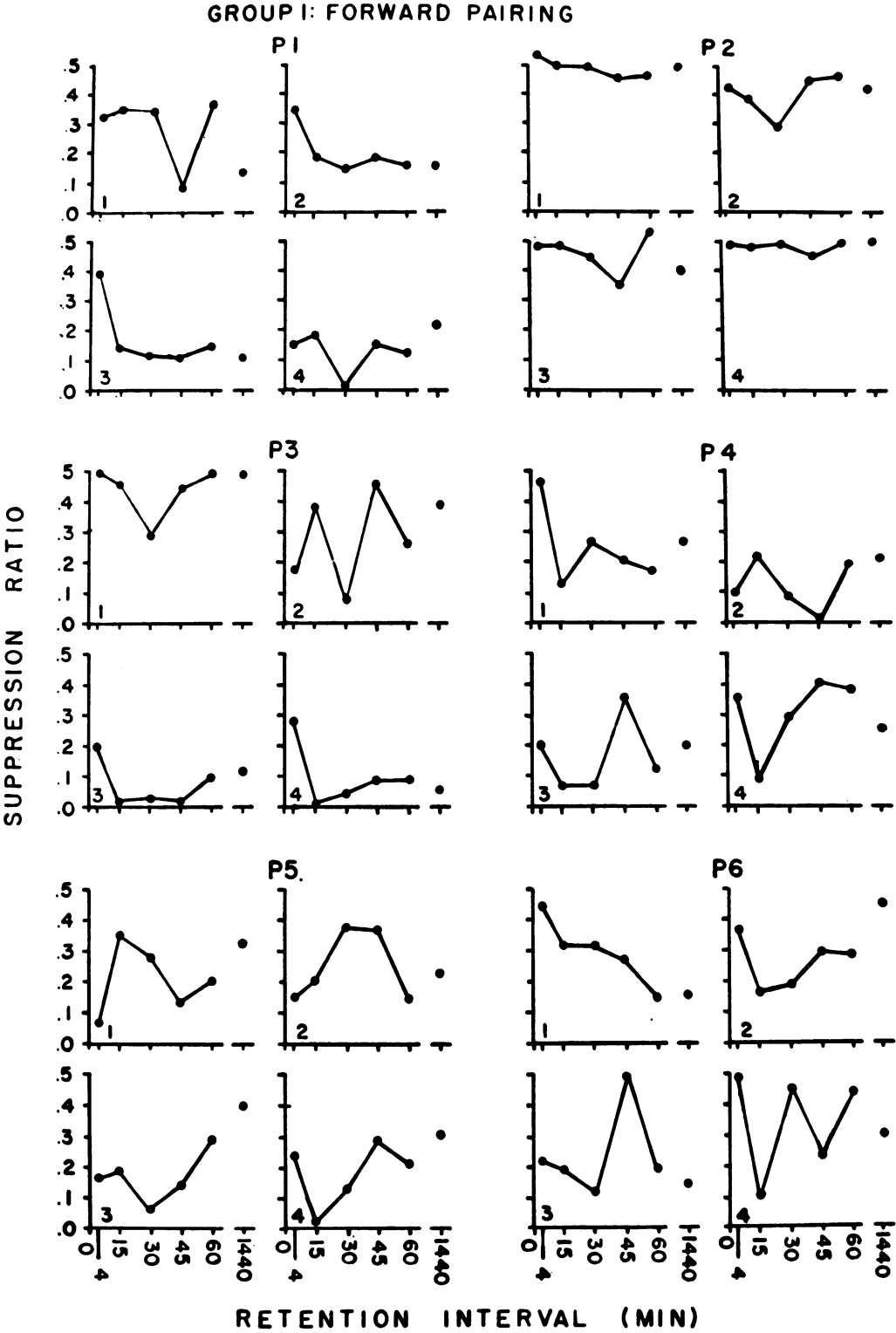


Fig. 3. The level of response suppression as a function of the testing interval for each replication in the forward pairing group.

rate occurred as a function of time. No significant effect of the retention interval on pretone responding was obtained ($F_{5,50} = 0.18$, $p > 0.10$). A significant effect, however, was obtained between groups ($F_{1,10} = 6.57$, $p < 0.05$). This group effect resulted from the higher level of responding in the forward pairing with operant delay group, as compared with the forward pairing group.

The results of the backward pairing group are shown in Figure 5. Suppression was minimal in this group and the rate of responding during the tone was roughly constant across retention intervals. All pigeons in this group show relatively flat functions. The results from the truly random group are shown in Figure 6. One pigeon in this group was dropped for failure to respond during the operant phase. Two of the remaining five pigeons, P21 and P23 show no suppression and flat functions.

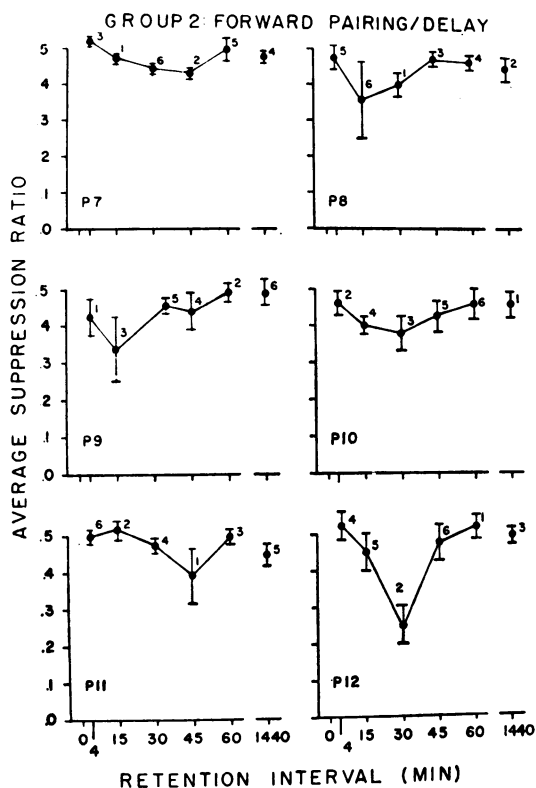


Fig. 4. The level of response suppression as a function of the testing interval for individual pigeons in the forward pairing with operant delay group. Each point represents the average suppression ratio for the four tests. The order of testing for each pigeon is represented by the numbers above the data points. The variability bands represent the standard error of the mean.

Table 1

Average response rate during the tone and pretone periods.

Group	Retention Intervals (Min)					
	4	15	30	45	60	1440
F						
Pretone	72 ^a	76	74	72	72	73
Tone	36	28	24	31	28	30
FD						
Pretone	111	115	113	110	113	109
Tone	103	95	88	92	108	99
B						
Pretone	54	51	51	46	53	48
Tone	53	47	50	47	49	48
R						
Pretone	44	57	51	50	50	49
Tone	34	35	30	29	32	45

^aResponse rate is in responses per minute.

Three pigeons, P19, P20, and P22 show both suppression to the tone and U-shaped functions. The interval of maximum suppression for these pigeons varied from 15 min to 45 min. Thus, when suppression was obtained in the truly random group, the resulting functions were similar to those obtained for the forward pairing groups while, when no suppression was obtained, the functions were similar to those obtained with the backward pairing group.

Group averages are compared in Figure 7. Due to the varied results obtained with the truly random group, its group average is not included in this figure. For both the forward pairing group and the forward pairing with operant delay group, the average point of maximum suppression occurred at the 30-min retention interval. The suppression level for the 1440-min retention interval approximately equalled the amount of suppression at the 60-min retention interval. A T test between the 60-min interval and the 1440-min interval was found to be nonsignificant for both the forward pairing group ($T_5 = 0.69$, $p > 0.10$) and the forward pairing with operant delay group ($T_5 = 1.67$, $p > 0.10$).

DISCUSSION

The U-shaped function obtained by Kamin (1957) showed a decrease in avoidance responding at intermediate retention intervals; in the present study, the U-shaped function showed an increase in suppression at inter-

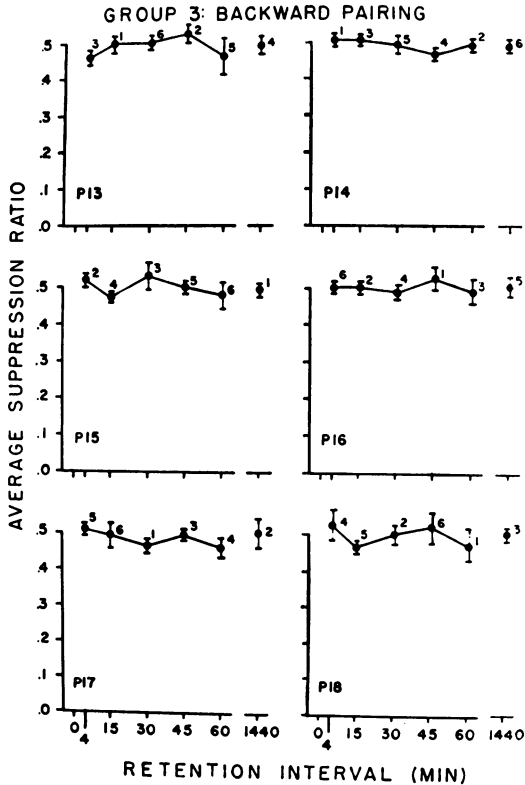


Fig. 5. The level of response suppression as a function of the testing interval for individual pigeons in the backward pairing group. Each point represents the average suppression ratio for the four tests. The order of testing for each pigeon is represented by the numbers above the data points. The variability bands represent the standard error of the mean.

mediate intervals. Changes in suppression, then, show an inverse relationship to changes in active avoidance responding. This finding may have implications for particular interpretations of the "Kamin effect" phenomenon. The decrement in active avoidance responding at intermediate retention intervals has been attributed to either a memory retrieval failure or to a direct interference with the avoidance response. The retrieval failure interpretation (Klein and Spear, 1970) assumes that the organism cannot retrieve from memory the associations learned during training. A "state-dependent" learning effect is considered the mechanism responsible for this retrieval failure. The organism learns the avoidance task under a particular internal state, which changes during the retention interval. The ability to retrieve the avoidance task is a function of the difference between the internal

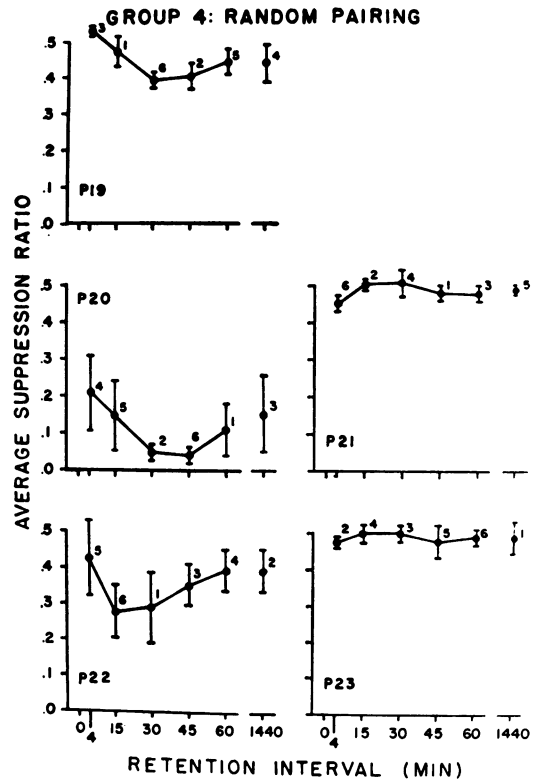


Fig. 6. The level of response suppression as a function of the testing interval for individual pigeons in the truly random group. Each point represents the average suppression ratio for the four tests. The order of testing for each pigeon is represented by the numbers above the data points. The variability bands represent the standard error of the mean.

state at testing and the internal state during training. At intermediate retention intervals, when internal cues are assumed to be maximally different from those during training, the animal is unable to retrieve the avoidance response or CS-US associations (Bryan and Spear, 1976). This position would assume that suppression, which reflects retrieval of CS-US associations, would decrease at intermediate retention intervals. In the present study, however, suppression increased at intermediate intervals. It is difficult to see how a decrease in retrieval would be reflected in an increase in suppression.

Performance interpretations do not have difficulty with an inverse relationship between avoidance responding and suppression. Those factors that interfere with the avoidance response can be assumed also to interfere with the baseline response in a suppression test.

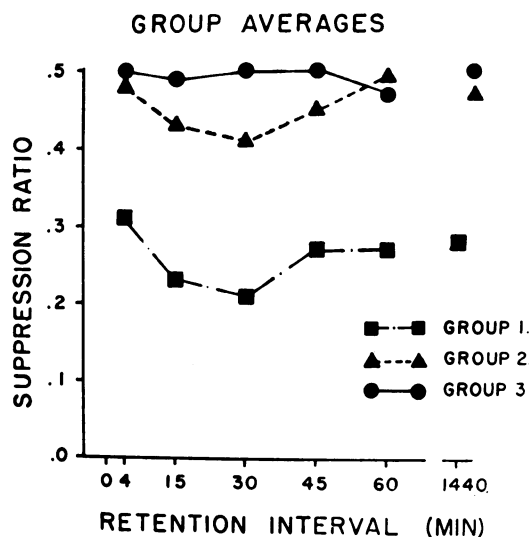


Fig. 7. Group averages showing the level of response suppression as a function of the testing interval for the forward pairing group (Group 1), the forward pairing with operant delay group (Group 2), and the backward pairing group (Group 3).

One performance interpretation (Anisman, 1975), however, runs into another difficulty with the present results. This position attributes the "Kamin effect" to a decrease in the organism's ability to initiate voluntary responses at intermediate retention intervals. Response inhibition results from changes in the level of various neuro-transmitters produced by the organism's direct exposure to an aversive US. The effect is independent of any association formed during training and is expected to occur following any exposure to an aversive stimulus of sufficient strength. This position would assume that the response rate in the operant phase of the present study would show systematic changes in the absence of the tone. The results, however, did not support this prediction; no systematic changes in the pretone response rate as a function of time were observed.

A performance interpretation by Denny (1958) does not encounter this problem. This model assumes that fear reactions elicited by the CS increases over the retention interval to an asymptotic level. Fear then gradually dissipates to a base level approximately equal to the level of fear during initial training. If retraining of the avoidance response occurs when fear is at a maximum level, the animal reacts to the CS and situational cues with fear

reactions, such as freezing (Stein, Hoffman, and Stitt, 1971), which are incompatible with the appropriate avoidance response. In the present study, presentation of the tone during testing may elicit fear responses that are incompatible with the key-peck response. Conditioned suppression has, in fact, often been assumed to reflect the conditioning of a central motivational state such as fear (Estes, 1969; Konorski, 1967; Mowrer, 1960; Rescorla and Solomon, 1967). The increase in suppression at intermediate retention intervals can, therefore, be viewed as reflecting an incubation of fear effect.

The lack of U-shaped functions in previous studies on conditioned suppression probably led most researchers to omit consideration of the organism's reaction to a CS over time. The reason McMichael (1966) and Tarpy (1966) did not obtain U-shaped functions is not entirely clear. The considerable number of differences in design between the present study and these previous studies makes direct comparison difficult. Pilot work had suggested that the opportunity to respond on the operant task during the retention interval might affect the type of gradient obtained during testing. The forward pairing with operant delay group, however, did not have the opportunity to respond during the retention interval, and still produced U-shaped functions. This result suggests that responding during the retention interval is not a critical factor. One possible problem with the McMichael (1966) and Tarpy (1966) studies was suggested by Brush (1971). He argued that the use of a chamber in testing different from the one used in training could result in a stimulus generalization decrement. McAllister and McAllister (1971) demonstrated such an effect when a different chamber was used for testing in an escape from fear paradigm. This problem may have been offset in our pilot study by placing the rats in the operant chamber immediately following shuttlebox training. The McAllisters have demonstrated that the degree of deficit in performance resulting from stimulus generalization is a function of delay between training and testing.

The present study clearly demonstrated that U-shaped functions can be obtained using conditioned suppression. The average point of maximum suppression, however, occurred at the 30-min retention interval; Kamin (1957)

obtained the greatest decrease in performance at the 60-min retention interval. It is possible that this difference reflects an underlying difference between avoidance responding and reactions to a CS. It is more parsimonious at present, however, to assume that this difference results from species and design variables. The interval where the minimum of the U-shaped function occurs has been found to vary as a function of the design used (reviewed by Brush, 1971) and as a function of the species used (reviewed by Squire, 1975).

The most obvious difference in the present study, as compared to previous studies on the Kamin effect, other than the use of conditioned suppression, was the use of a within-subjects design. This design permitted an evaluation of time-dependent changes in conditioned suppression within individual pigeons. The results showed that the point of maximum suppression varied from 15 min to 45 min across pigeons. This variance in the U-shaped function has not been detected in previous studies, which have reported only group averages. The successful use of the within-subjects design indicates that U-shaped functions can be obtained when animals are trained to asymptotic levels. The results showed that pigeons in the forward pairing group produced U-shaped functions for the fourth replication of the testing sequence after over 30 sessions of Pavlovian conditioning. This result argues against any interpretation of the Kamin effect, which relies on associative factors during acquisition. To account for U-shaped functions with conditioning at asymptotic levels, the retrieval failure model must assume that a CS cannot reach sufficient strength to act as an appropriate retrieval cue.

There was some question in the present study about the appropriate control group to use for Pavlovian conditioning. A comparison of the results for the backward pairing group and the truly random group showed a lack of conditioning for the former group but the presence of conditioning and U-shaped functions for three pigeons in the later group. Rescorla (1972) predicted initial conditioning using the truly random procedure, which then dissipates with continued training. Pigeons that showed conditioning in the truly random group, however, continued to suppress responding during the tone after over 30 Pavlovian conditioning sessions. Therefore, it

seems unlikely that the conditioning demonstrated in these pigeons was a transitory effect. The reason some pigeons in the truly random group showed conditioning and some pigeons did not, may have to do with the number of chance forward pairings each pigeon received. It seems likely, however, that there would have been only negligible differences in the total number of forward pairings between pigeons, given the number of training sessions. Benedict and Ayres (1972) have shown that random schedules with forward pairings occurring at the beginning of training are more likely to result in conditioning. In another study, Ayres, Benedict, and Witcher (1975) found that the total number of chance pairings contributed to the presence or absence of conditioning. They also found that the absence of conditioning to the CS was significantly related to the number of shock presentations before the initial chance pairings of the CS with shock. It seems likely that the difference in conditioning between pigeons in the truly random group was the result of both the number of chance pairings that occurred during the early sessions of training and the number of shock presentations that occurred before the first chance pairing.

The forward pairing group and the forward pairing with operant delay group both produced U-shaped functions. The lower level of total suppression observed in the forward pairing with operant delay group was unexpected, however. This group also showed a significantly higher rate of responding during the pretone period. It is possible that the higher rate of responding in this group represents a contrast effect resulting from the imposition of a delay period between the Pavlovian and operant phases. The higher rate of responding may, in turn, have led to an attenuation of response suppression during the tone.

REFERENCES

- Anisman, H. Time-dependent variations in aversively motivated behaviors: Nonassociative effects of Cholinergic and Catecholaminergic activity. *Psychological Review*, 1975, **82**, 359-385.
- Ayres, J. J. B., Benedict, J. O., and Witcher, E. S. Systematic manipulation of individual events in a truly random control in rats. *Journal of Comparative and Physiological Psychology*, 1975, **88**, 97-103.
- Azrin, N. H. A technique for delivering shock to pigeons. *Journal of the Experimental Analysis of Behavior*, 1959, **2**, 161-163.

- Benedict, J. O. and Ayres, J. B. Factors affecting conditioning in the truly random control procedure in the rat. *Journal of Comparative and Physiological Psychology*, 1972, **78**, 323-330.
- Brush, F. R. Retention of aversively motivated behavior. In F. R. Brush (Ed), *Aversive conditioning and learning*. New York: Academic Press, 1971. Pp. 405-465.
- Bryan, R. G. and Spear, N. E. Forgetting of a discrimination after intervals of intermediate length: The Kamin effect with choice behavior. *Journal of Experimental Psychology: Animal Behavior Processes*, 1976, **2**, 221-234.
- Denny, M. R. The "Kamin effect" in avoidance conditioning. *American Psychologist*, 1958, **13**, 419.
- Estes, W. K. Outline of a theory of punishment. In B. A. Campbell and R. M. Church (Eds), *Punishment and aversive behavior*. New York: Appleton-Century-Crofts, 1969. Pp. 57-82.
- Hunt, H. F. and Brady, J. V. Some effects of electroconvulsive shock on a conditioned emotional response (Anxiety). *Journal of Comparative and Physiological Psychology*, 1951, **44**, 88-89.
- Kamin, L. J. Retention of an incompletely learned avoidance response. *Journal of Comparative and Physiological Psychology*, 1957, **50**, 457-460.
- Kamin, L. J. Trace conditioning of the conditioned emotional response. *Journal of Comparative and Physiological Psychology*, 1961, **54**, 149-153.
- Klein, M. and Rilling, M. Generalization of free-operant avoidance behavior in pigeons. *Journal of the Experimental Analysis of Behavior*, 1974, **21**, 75-88.
- Klein, S. B. and Spear, N. E. Forgetting by the rat after intermediate intervals (Kamin effect) as retention failure. *Journal of Comparative and Physiological Psychology*, 1970, **71**, 165-170.
- Klein, S. B. and Spear, N. E. Sequential variables and the Kamin effect. *Learning and Motivation*, 1973, **4**, 357-365.
- Konorski, J. *Integrative activity of the brain*. Chicago: University of Chicago Press, 1967.
- Kremer, E. F. and Kamin, L. J. The truly random control procedure: Associative or non-associative effects in the rat. *Journal of Comparative and Physiological Psychology*, 1974, **74**, 203-210.
- McAllister, W. R. and McAllister, D. E. Behavioral measurements of conditioned fear. In F. R. Brush (Ed), *Aversive conditioning and learning*. New York: Academic Press, 1971. Pp. 150-182.
- McMichael, J. S. Incubation of anxiety and instrumental behavior. *Journal of Comparative and Physiological Psychology*, 1966, **61**, 208-211.
- Mowrer, O. H. *Learning theory and behavior*. New York: Wiley, 1960.
- Quinsey, V. L. Conditioned suppression with no CS-US contingency in the rat. *Canadian Journal of Psychology*, 1971, **25**, 69-82.
- Rescorla, R. A. Conditioned inhibition of fear. In M. J. Mackintosh and W. K. Honig (Eds), *Fundamental issues in associative learning: proceedings of a symposium held at Dalhousie University, Halifax, June, 1968*. Halifax: Dalhousie University Press, 1969.
- Rescorla, R. A. Informational variables in Pavlovian conditioning. In G. H. Bower (Ed), *The psychology of learning and motivation: advances in research and theory*, Vol. 6. New York: Academic Press, 1972.
- Rescorla, R. A. and Solomon, R. L. Two-process learning theory: Relationship between Pavlovian conditioning and instrumental learning. *Psychological Review*, 1967, **74**, 151-182.
- Squire, L. R. Short-term memory as a biological entity. In D. Deutsch and J. A. Deutsch (Eds), *Short-term memory*. New York: Academic Press, 1975.
- Stein, N., Hoffman, H. S., and Stitt, C. Collateral behavior of the pigeon during conditioned suppression of key pecking. *Journal of the Experimental Analysis of Behavior*, 1971, **15**, 83-93.
- Tarpy, R. Incubation of anxiety as measured by response suppression. *Psychonomic Science*, 1966, **4**, 189-190.

Received 6 January 1977.

(Final acceptance 7 September 1977.)